

Polar Biosci., 14, 10–23, 2001

Variation in the diatom community under fast ice near Syowa Station, Antarctica, during the austral summer of 1997/98

Akira Ishikawa^{1*}, Naoki Washiyama², Atsushi Tanimura¹
and Mitsuo Fukuchi³

¹ Faculty of Bioresources, Mie University, 1515 Kamihama-cho, Tsu 514-8507

² Ryokuseisha Corp., Tsukiji Yasuda Bldg. 15–14, Tsukiji 2-chome, Chuo-ku, Tokyo 104-0045

³ National Institute of Polar Research, Kaga 1-chome, Itabashi-ku, Tokyo 173-8515

Abstract: Variations in abundance and community structure of diatoms under the fast ice near Syowa Station were investigated almost daily during the austral summer of 1997/98. Two periods of high chlorophyll *a* concentration were observed throughout the study: from the end of December to early January and from the middle to the end of January. Size fractionation of chlorophyll *a* revealed that phytoplankton during the former period consisted mostly of organisms larger than 20 μm and during the latter period, 10–20 μm . The large diatoms, *Porosira pseudodenticulata* and *Pseudonitzschia turgiduloides*, and small diatoms, *Fragilariopsis* spp., were the dominant organisms in the former and latter periods, respectively. Melting of the fast ice occurred in January, indicating a possibility that small sized diatoms were released from the ice to the water column. Accumulation of small diatoms in a sediment trap followed a decrease of their abundance in the water column. These results indicate that most of the ice algae detached from the ice sank directly to the bottom during the latter half of the austral summer.

key words: chlorophyll *a*, diatom community, water column, sinking, Syowa Station

Introduction

The importance of ice algae, as primary producers, in ice-covered areas is well known (Horner, 1985a). Their abundance in the ice increases in spring, before phytoplankton blooms in the water column (e.g., Horner, 1985a,b). There are reports that the ice algae released from the ice seed the bloom in the water column, especially in ice edge zones (Garrison and Buck, 1985; Smith and Nelson, 1985; Garrison *et al.*, 1987). However, Riebesell *et al.* (1991) contend that grazing and sinking are the main fates of sea ice biota.

Studies on ice algae near Syowa Station have been undertaken since the late 1950s (Hoshiai and Watanabe, 1996). Near Syowa the ice algal biomass reaches a maximum in spring/early summer (Hoshiai, 1981a,b; Watanabe and Satoh, 1987) and the abundance of phytoplankton in the water column usually reaches its maximum at the end of January and in early February (e.g., Satoh *et al.*, 1986). The primary production of the phytoplankton in the water column is lower than that of the ice algae in the spring but higher in the summer (Satoh and Watanabe, 1988; Satoh *et al.*, 1991).

* E-mail: ishikawa@bio.mie-u.ac.jp

In this study we report almost daily changes in the community structure of phytoplankton with special reference to that of diatoms under the fast ice near Syowa Station during the austral summer of 1997/98.

Materials and methods

Sampling was conducted at St. A ($69^{\circ}00.00'N$, $39^{\circ}37.12'E$), located near Syowa Station, from 27 December, 1997 to 3 February, 1998 (Fig. 1). The water depth at the station was 40 m. The thickness of the fast ice at the site was 260 and 215 cm at the start and at the end of the sampling period, respectively. The ice in this season was thicker than is usually observed at the site by more than 1 m (e.g., Watanabe and Satoh, 1987). Water samples were collected with a 2 l Niskin bottle through a hole drilled in the ice. Collections were made almost daily at 1 m depth (daily water samples) and at approximately weekly intervals at 1, 5, 10, 20 and 35 m depths (vertical water samples) below the ice. Temperature and salinity were measured with a CTD (Sea-Bird Electronics, Inc). The CTD operation was done almost daily at depths shallower than several meters and at approximately weekly intervals through the water column.

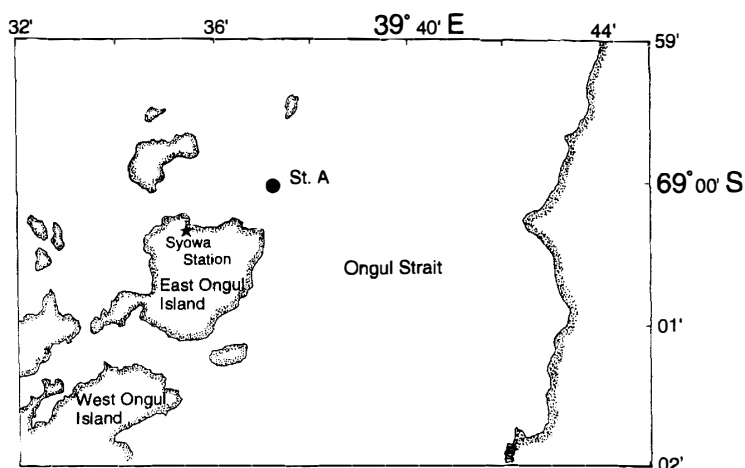


Fig. 1. Location of sampling station near Syowa Station, Antarctica.

Concentration of chlorophyll *a* was determined for each water sample. A 200 ml aliquot from both daily and vertical water samples was filtered through a Whatman GF/F glass fiber filter with vacuum pressure of less than 100 mmHg to give total Chl *a*. Another aliquot (300–500 ml) of daily water sample was filtered through a $20\mu\text{m}$ mesh ($>20\mu\text{m}$ fraction) without vacuum and the filtrate was sequentially filtered through a Nuclepore filter with pore size of $10\mu\text{m}$ ($10\text{--}20\mu\text{m}$ fraction) without vacuum. The chlorophyll *a* retained on the filters was extracted in *N,N*-dimethylformamide at -20°C for 24 h (Suzuki and Ishimaru, 1990) and its concentration was determined by the fluorometric method of Parsons *et al.* (1984) with a Turner Design fluorometer Model 10-AU-005. Chlorophyll *a* concentration of the $<10\mu\text{m}$ fraction was obtained from the difference between the total Chl *a* and the sum of the $>10\mu\text{m}$ fraction. Size fractionation of chlorophyll *a* for the vertical water samples was done using only the

20 μm mesh ($>$ or $<$ 20 μm fractions).

The daily water samples were also used for cell counts of diatoms and dinoflagellates. Those samples were immediately fixed by adding borax buffered formaldehyde at a final concentration of 2%. A 50 ml aliquot of the sample was settled in an Utermöhl chamber for at least 24 h; species identification and cell counts were done with a Nikon TE-300 inverted microscope at 100–400 \times magnification and, when necessary for positive identification of species, cells were cleaned with concentrated HCl and KMnO_4 mixture (Simonsen, 1974), dried in air, placed on aluminum stubs, coated with gold, and examined with a scanning electron microscope (JEOL, JSM-T-200). The species was identified by referring to Medlin and Priddle (1990) and Hasle and Syvertsen (1997). Among the diatom population, the two dominant species were selected to determine species succession. In this analysis, the two dominant species almost always occupied more than 80% of the total diatom population.

Sinking diatoms were collected with a sediment trap moored 20 m below the ice. The sediment trap was 70.6 cm in height; upper 40.6 cm cylinder, with a baffle at the top, and lower 30 cm funnel with 500 ml bottle at the bottom. The diameter was 15.4 cm, making a collecting area of 186 cm^2 . The collection was made during the period from 2 January to 2 February 1998. The traps were filled with artificial sea water with salinity of *ca.* 35 g l^{-1} and borax buffered formaldehyde just before deployment. The trap was replaced at approximately weekly intervals. For species identification and counting of diatoms, a 1/250–1/500 aliquot of the deposited matter was suspended in 10 ml of filtered sea water containing borax buffered formaldehyde at 2%. From this suspension, a 1 to 2 ml aliquot was put on a slide glass and cells counted at 100–400 \times magnification. Counts were carried out in triplicate for each sample and the daily cell flux ($\text{cells m}^{-2} \text{ day}^{-1}$) was calculated. Although the cell flux is illustrated only for dominant diatoms in this study, these species occupied most (83–98%) of the total diatom cells.

Results

Temperature, salinity and density

A vertical profile of temperature showed that the thermocline appeared after 3 January and deepened to the end of January (Fig. 2A). Warm water exceeding 0°C seemed to be located from shallow to deeper layers as the thermocline deepened. Maximum temperature was recorded (0.25°C) at 1 m below the ice on 17 January.

The vertical salinity gradient was very small in the water column from the end of December to the beginning of January (Fig. 2B). Thereafter, the gradient gradually appeared at depths shallower than 15 m and developed throughout the water column by the end of January. Minimum salinity was recorded (31.4 PSU) at 1 m below the ice on 25 January. The trend of changes in salinity seemed to be opposite to that in temperature, indicating that melting of the fast ice occurred.

The water density was almost homogeneous in the water column deeper than 1 m below the ice until the beginning of January (Fig. 2C). A density gradient was formed in the surface layer shallower than around 10 m on 7 January and developed through the water column by the end of January. No apparent pycnocline was observed.

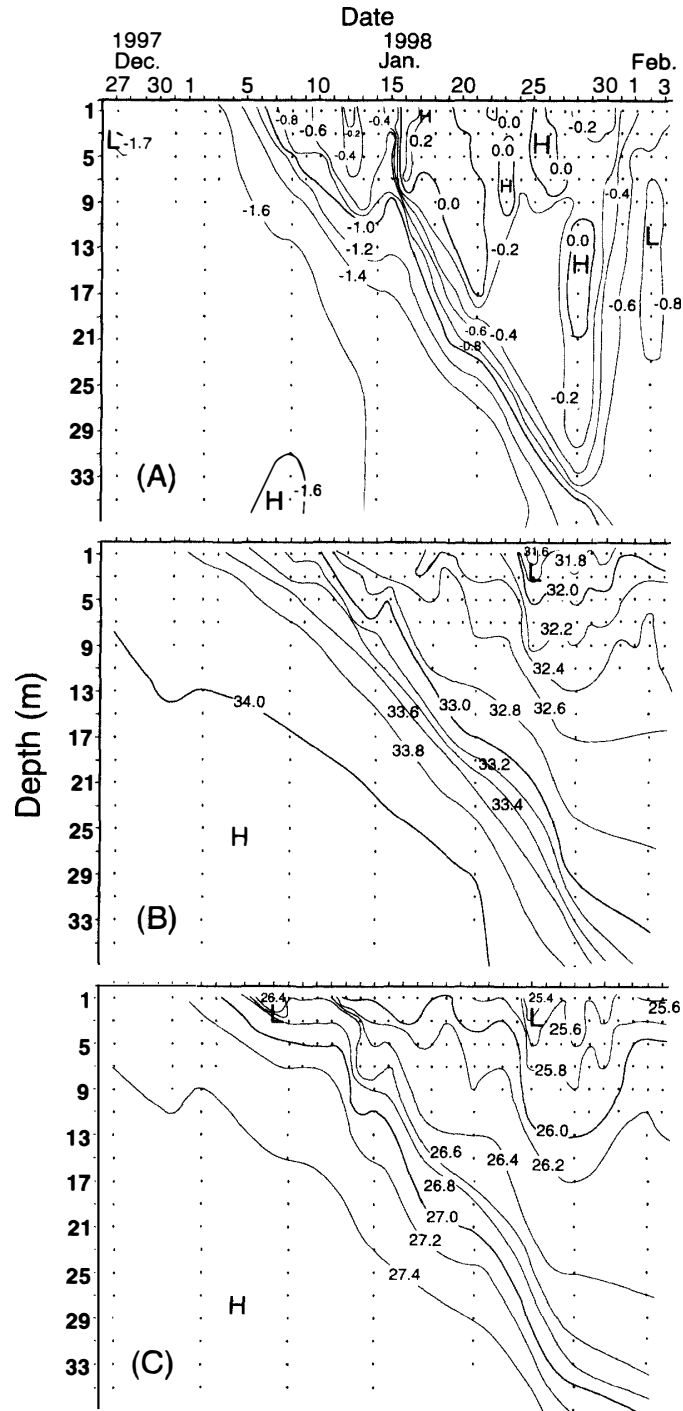


Fig. 2. Temporal variations of (A) temperature, (B) salinity and (C) density, σ_t , in the water column from 1 m below the fast ice to near the bottom at St. A from 27 December 1997 to 3 February 1998.

Chlorophyll *a*

Throughout the study, two periods of high Chl *a* concentration were observed in layers shallower than 20 m: the first from late December to early January and the second

from mid- to late January (Fig. 3A). Total Chl *a* showed a trend of decreasing gradually with depth. Detailed changes in total Chl *a* 1 m below the ice are shown in Fig. 4A. Concentration of total Chl *a* increased from the beginning of the study to 30 December ($7.9 \mu\text{g l}^{-1}$), decreasing to $1.3 \mu\text{g l}^{-1}$ on 10 January. Total Chl *a* increased again from 14 January, reaching the highest value of $9.9 \mu\text{g l}^{-1}$ on 22 January. The high abundance lasted for about 7 days, then decreased until the end of the study.

The fraction $>20 \mu\text{m}$ accounted for more than 90% of the total Chl *a* through the water column at the end of December but decreased to $<10\%$ at the end of January (Fig. 3B). Detailed changes in relative abundance of the fractions to the total Chl *a* at 1 m below the ice are also shown in Fig. 4B. The fraction $>20 \mu\text{m}$ comprised 50–90%, from the end of December to the beginning of January, decreasing later in the season (Fig. 4B). The 10–20 μm fraction increased, supplanting the $>20 \mu\text{m}$ fraction, from the beginning of January, and became the major component of the total Chl *a* by the middle of January. Thereafter, this fraction comprised almost 60–90% of the total Chl *a*. Throughout the study period, the fraction of $>10 \mu\text{m}$ (sum of >20 and 10–20 μm) accounted for 62–99% of the total Chl *a*, except in a few samples (30 December,

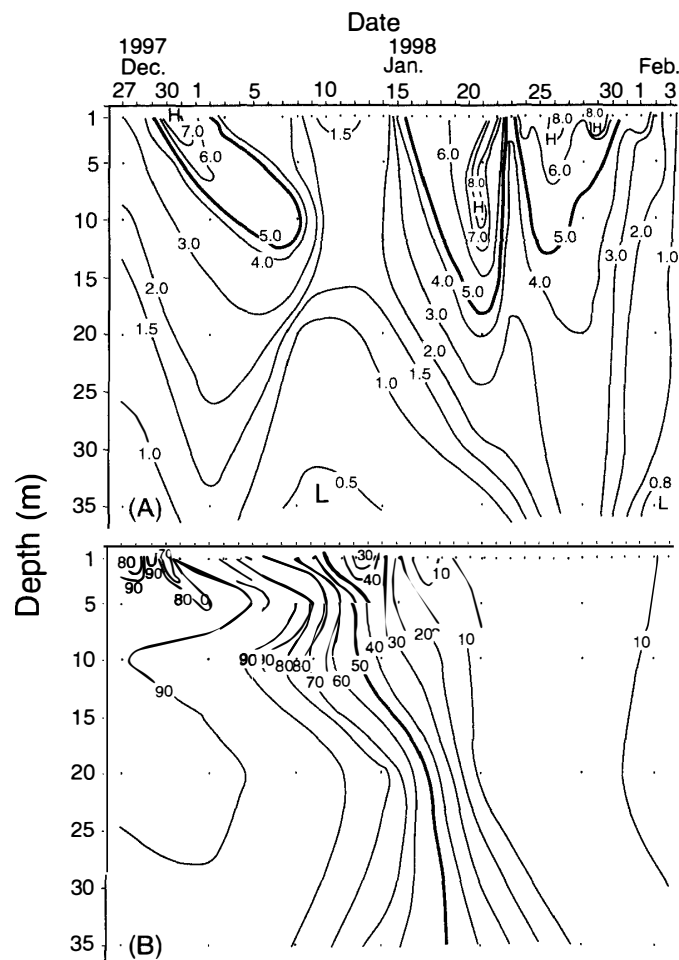


Fig. 3. Temporal variations of (A) total chlorophyll *a* concentration ($\mu\text{g l}^{-1}$), and (B) relative abundance (%) of fraction larger than $20 \mu\text{m}$ in the water column at St. A.

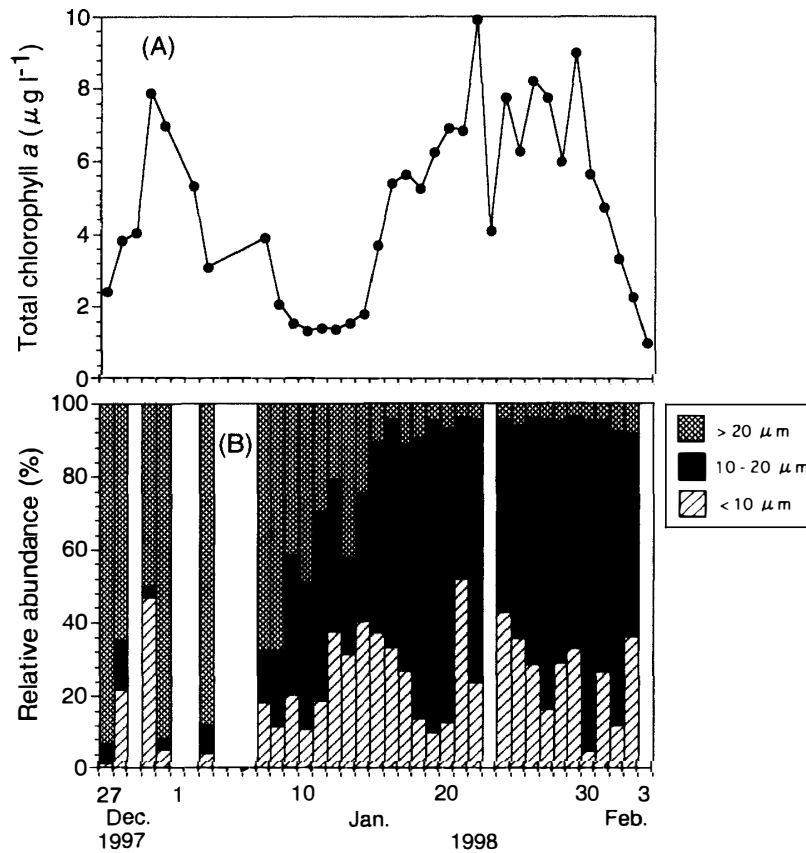


Fig. 4. Daily changes in (A) total chlorophyll *a* concentration and (B) relative abundance of its size fractions at 1 m below the ice in the water column at St. A. Unfilled parts denote no data.

and 21 and 24 January). No obvious trend in the change of relative abundance of the fraction smaller than $10\mu\text{m}$ was observed.

Diatom and dinoflagellate community structure

Daily change in cell abundance of total diatoms at 1 m below the ice (Fig. 5A) was generally similar to that of total Chl *a* at that depth. Namely, high abundances of $>10^5$ cells l^{-1} were observed before and after the low abundance (3×10^4 – 9.6×10^4 cells l^{-1}) period from 9 to 13 January 1998. The abundance exceeded the order of 10^6 cells l^{-1} from the middle to the end of January. On the other hand, abundance of the total dinoflagellates (Fig. 5B) was always much lower, at a density from 0– 10^3 cells l^{-1} , than that of diatoms. Almost 100% of the species observed in the dinoflagellate population were *Protoperidinium* spp., which are heterotrophic. Centric diatoms were observed at the relative abundance of 9–10% of the total diatom population from 27 December to 3 January. The relative abundance decreased thereafter to $<1\%$ by 12 January. Instead, pennate diatoms occupied nearly or totally the diatom populations after 7 January. In this study, 11 species of 8 genera of centric diatoms were observed (Table 1). Among them, the large species, *Porosira pseudodenticulata* ($53.9\mu\text{m}$ in average diameter; $n=106$), was almost always the dominant species at a relative abundance of 69–100% of the centric diatom population before the middle of January (Fig. 6A).

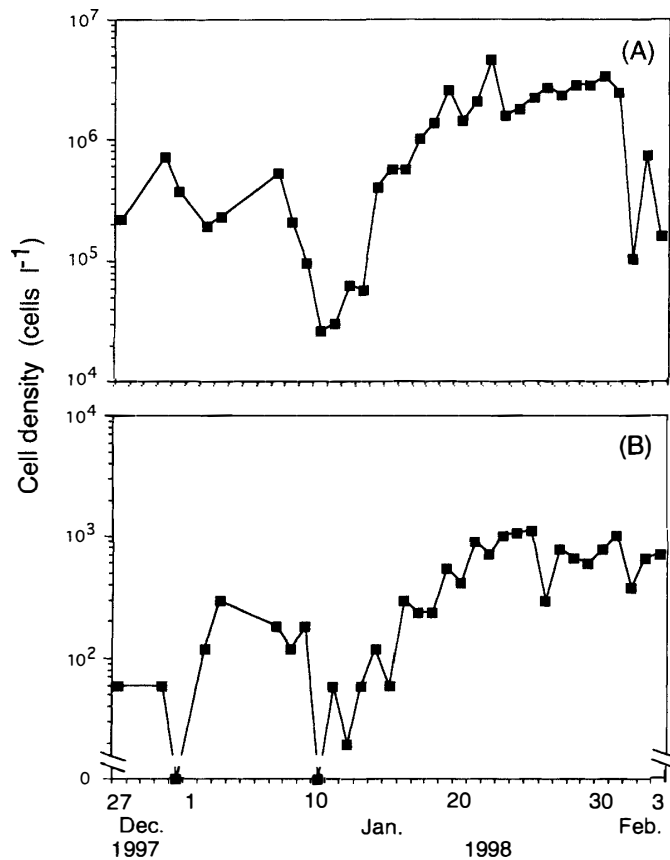


Fig. 5. Daily changes in cell densities of (A) diatoms and (B) dinoflagellates at 1 m below the ice in the water column at St. A.

The pennate diatom population, in which 8 species and 3 unidentified groups of 7 genera were observed (Table 1), was characterized by the large species, *Pseudo-nitzschia turgiduloides* (94.9 and 2.6 μm in average for the apical and transapical axes, respectively; $n = 103$), and the small species, *Fragilariopsis curta* and *F. cylindrus* (23.5 and 2.5 μm in average for the apical and transapical axes, respectively; $n = 106$) (Fig. 6B). The *Fragilariopsis* species were counted as a single taxon (*Fragilariopsis* spp.) because the two species were not distinguishable by light microscopy. *Pseudo-nitzschia turgiduloides* was the dominant species, at a relative abundance of 47–99%, from 27 December to 8 January and *Fragilariopsis* spp., at a relative abundance of 50–100%, during the rest of the study period, except on 13 January. In this study, *P. turgiduloides* often formed long chains, whereas most cells of *Fragilariopsis* spp. were solitary or in short chains of 2–3 cells. Aggregates were often observed in the water samples.

As a result of analysis in relationships between the cell densities of the dominant diatoms and concentration of the >20 and 10–20 μm chlorophyll *a* fractions at 1 m below the ice, *P. pseudodenticulata* and *P. turgiduloides* showed significant positive relationships with the >20 μm fraction; the correlation coefficients (r^2) were 0.78 ($p < 0.001$) and 0.57 ($p < 0.001$), respectively (Table 2). On the other hand, a highly significant positive relationship ($r^2 = 0.80$, $p < 0.001$) was found between *Fragilariopsis* spp. and the 10–20 μm fraction.

Table 1. List of species of diatoms observed at 1 m below the fast ice in the water column at St. A during the period from 27 December, 1997 to 3 February, 1998.

Diatoms	
Centrales	
<i>Actinocyclus</i>	<i>actinochilus</i> (Ehrenberg) Simonsen
<i>Chaetoceros</i>	sp. 1
<i>C.</i>	sp. 2
<i>Coscinodiscus</i>	<i>asteromphalus</i> Ehrenberg
<i>C.</i>	sp.
<i>Eucampia</i>	<i>antarctica</i> (Castracane) Mangin
<i>Porosira</i>	<i>pseudodenticulata</i> (Hustedt) Jousé
<i>Rhizosolenia</i>	sp.
<i>Stellarima</i>	<i>microtrias</i> (Ehrenberg) Hasle & Sims
<i>Thalassiosira</i>	<i>australis</i> M. Peragallo
<i>T.</i>	<i>tumida</i> (Janisch) Hasle
Pennales	
<i>Fragilariopsis</i>	<i>curta</i> (Van Heurck) Hustedt
<i>F.</i>	<i>cylindrus</i> (Grunow) Krieger
<i>Navicula</i>	<i>directa</i> (W. Smith) Ralfs
<i>N.</i>	<i>glaciei</i> Van Heurck
<i>N.</i>	spp.
<i>Nitzschia</i>	<i>stellata</i> Manguin
<i>N.</i>	spp.
<i>Pinnularia</i>	<i>quadratarea</i> var. <i>constricta</i> (Østrup) Heiden
<i>Pleurosigma</i>	<i>directum</i> Grunow
<i>Pseudo-nitzschia</i>	<i>turgiduloides</i> (Hasle) Hasle
<i>Stauroneis</i>	spp.

Sinking diatoms

Of the dominant diatoms, the two large species, *P. pseudodenticulata* and *P. turgiduloides*, and the small species of *Fragilariopsis* showed an opposite trend in cell flux at 20 m below the ice (Fig. 7). The cell fluxes of the two large species were high during the first half of January, with maxima just before the middle of January of 5.1×10^6 cells $\text{m}^{-2}\text{day}^{-1}$ for *P. pseudodenticulata* (Fig. 7A) and 1.5×10^8 cells $\text{m}^{-2}\text{day}^{-1}$ for *P. turgiduloides* (Fig. 7B). Thereafter, their cell fluxes decreased drastically to less than 2.5×10^5 and 2.8×10^7 cells $\text{m}^{-2}\text{day}^{-1}$, respectively, at the end of January. Although the cell flux of the small species was relatively modest at $< 1.8 \times 10^7$ cells $\text{m}^{-2}\text{day}^{-1}$ in the first half of January, it increased later and reached the maximum flux of 1.2×10^9 cells $\text{m}^{-2}\text{day}^{-1}$ from the end of January to the beginning of February (Fig. 7C). The cells deposited in the trap were well aggregated.

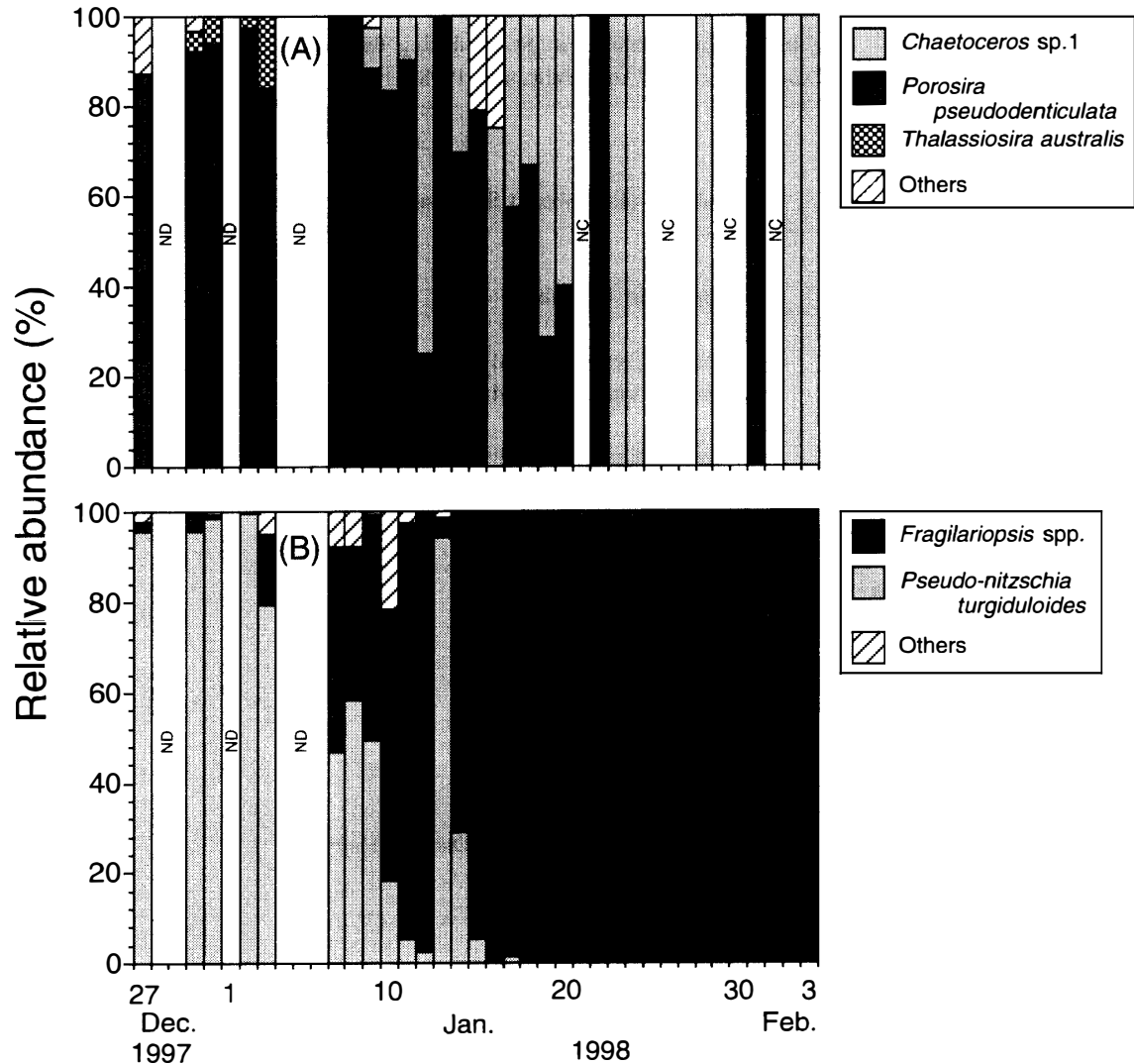


Fig. 6. Daily changes in relative abundance of the two dominant species among (A) centric and (B) pennate diatom populations at 1 m below the ice in the water column at St.A. ND and NC denote no data and no cells, respectively.

Table 2. Relationships between cell densities of 3 dominant diatoms and concentrations of size-fractionated chlorophyll *a* (10–20 μm and >20 μm) at 1 m below the ice. Coefficient of regression (r^2) in parenthesis. + and – denote positive and negative relationships, respectively.

Diatom species	Fraction of chlorophyll <i>a</i>	
	10–20 μm	>20 μm
<i>Porosira pseudodenticulata</i>	– (0.17) [‡]	+ (0.78) [*]
<i>Pseudo-nitzschia turgiduloides</i>	– (0.25) [‡]	+ (0.57) [*]
<i>Fragilariopsis</i> spp.	+ (0.80) [*]	– (0.18) [‡]

* Significant correlation, $p < 0.001$.

‡ Non significant correlation, $p > 0.1$.

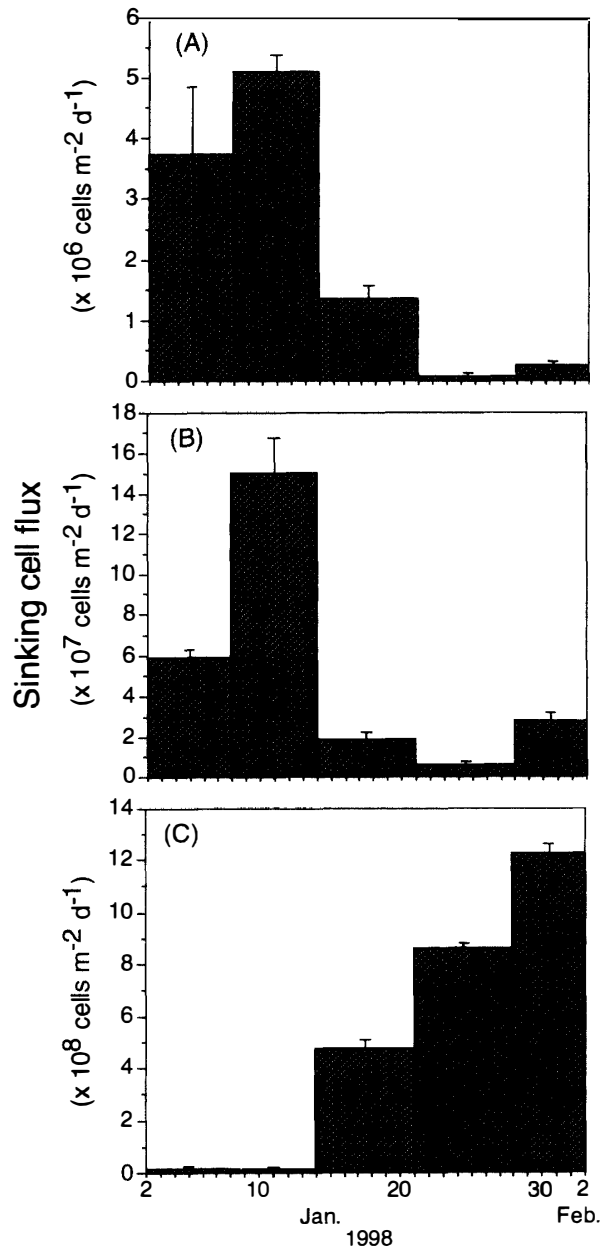


Fig. 7. Temporal changes in sinking cell fluxes of dominant diatoms, (A) *Porosira pseudodenticulata*, (B) *Pseudo-nitzschia turgiduloides* and (C) *Fragilariopsis* spp., monitored by sediment trap 20 m below the bottom of the fast ice at St. A from 2 January to 2 February 1998. Bars represent \pm SD. Note different scales on y-axes.

Discussion

In this study, the concentration of $>20\mu\text{m}$ chlorophyll *a* fraction at 1 m below the ice was related to the cell abundances of two large species, *P. pseudodenticulata* and *P. turgiduloides* (Table 2). A higher significant positive relationship was found for the former species although its cell abundance was much lower than that of the latter one.

This is probably due to the larger cell volume of the former species, which contains more chlorophyll *a* in a cell than the latter species. This indicates that during the first period of high total Chl *a* concentration, *i.e.*, from the end of December to early January, the two species represented the phytoplankton population and, furthermore, *P. pseudodenticulata* was the primary component of the total Chl *a*. These two diatoms commonly occur in the ice algal assemblage in the Antarctic (*e.g.*, Garrison and Buck, 1989; Garrison, 1991) and they have also been found in the sea ice around Syowa Station (Watanabe, 1982, 1988; Watanabe *et al.*, 1990). Apart from the ice, limited information (Watanabe, pers. commun.) about the species composition in the water column around the station shows that *P. pseudodenticulata* and *P. turgiduloides* occurred as dominant species among the diatom population from spring to early summer at the end of 1983 and the cell abundance of the latter species was much higher than that of the former species. His observation is similar to ours, suggesting the possibility that these species are major components of the diatom population in the water column in early summer around the station. On the other hand, a highly significant positive relationship between cell density of *Fragilariopsis* spp. and the concentration of the 10–20 μm chlorophyll *a* fraction at 1 m below the ice was found (Table 2), indicating that the main component in the phytoplankton population during the other period of high total Chl *a*, *i.e.*, from the middle to the end of January, was the small nano-sized pennate diatom. Those species were also observed to be dominating in the water column under the ice around Syowa Station in January 1984 (Watanabe, pers. commun.).

Iwanami *et al.* (1986) observed a development of chlorophyll *a* concentration at a pycnocline formed at shallower depth (*ca.* 1.3 m below the ice) near Syowa Station, from the middle to the end of January 1984, and suggested that the development was due to growth of phytoplankton at the shallower pycnocline which kept them from sinking to poorly lighted deeper layers for a longer time. In this study, instead of no appearance of an obvious pycnocline, a density gradient developed through the water column by the end of January (Fig. 2C). Furthermore, the apparent growth rate calculated from the change in diatom cell density (Fig. 5A), from 2.6×10^4 cells l^{-1} to 4.7×10^6 cells l^{-1} (the maximum value during the study) on 10 and 22 January, respectively, was much higher (0.43 d^{-1}) than the growth rate of the phytoplankton community on 16 January (0.18 d^{-1} ; Ishikawa, unpublished data), as estimated *in situ* (incubated at *ca.* 0.5 m below the ice) by the dilution method (Landry and Hassett 1982). This indicates that the development of the population at 1 m below the ice after 10 January cannot be explained only by the growth of the cells. *Fragilariopsis curta* and *F. cylindrus* are common and often dominate in the ice algal assemblage around Syowa Station (Watanabe, 1988; Watanabe *et al.*, 1990) and in other Antarctic regions (*e.g.*, Burkholder and Mandelli, 1965; Richardson and Whitaker, 1979; Garrison *et al.*, 1986; Garrison and Buck, 1989; Garrison, 1991). It has been reported that the abundance of chlorophyll *a* in the bottom ice decreases markedly in January with ice melt (Sasaki and Hoshiai, 1986; Watanabe *et al.*, 1990). Judging from the fact that the ice also melted in January, 1998, it can be strongly assumed that a large number of the cells of *Fragilariopsis* spp. were released into the water column from the bottom ice, where those species dominate over other populations of ice algal species. This is a major reason why the 10–20 μm fraction of chlorophyll *a* in terms of *Fragilariopsis* spp. populations

developed in the water column from the middle to the end of January. In other words, it is likely that most of the phytoplankton cells in the water column were derived from the ice, while they could still grow. Sasaki and Hoshiai (1986) reported that the ice algae detaching from the ice increased in late December, also indicating the possibility that the phytoplankton increase we observed at the end of December was a result of the increased detachment of ice algae from the ice.

It has been reported that the ice algae released from the ice are a seed for the bloom in the water column at the ice edge zone (Garrison and Buck, 1985; Smith and Nelson, 1985; Garrison *et al.*, 1987). On the other hand, it has also been suggested that the aggregated ice algae sink rapidly to the bottom and do not act as a seed for the bloom (Riebesell *et al.*, 1991). In this study, relatively higher concentration of total Chl *a* extended from the surface to the subsurface (Fig. 3A) and the sinking cell flux of the dominant species (Fig. 7) increased with decreasing chlorophyll *a* concentration (Figs. 3A and 4A), indicating that our results would be comparable with the latter scheme. According to Marchant *et al.* (1996), the organic materials (marine snow) collected by divers below the surface in the water column around Syowa Station in mid-January 1994 were dominated by diatoms and mucilage which derived from the ice community. Sasaki and Hoshiai (1986) also reported that the ice algae detached from the ice around the station sink directly to the bottom during summer and are not grazed during sinking. Thus, the algae reaching the bottom become a major food source for the benthic animals.

As a whole, abundance and community structure of diatoms varied drastically within the short summer of 1997/98. The variation was due predominantly to abiotic events, such as ice melting, rather than biotic events, such as growth of the phytoplankton. The hydrographic conditions during this summer, especially warm water exceeding 0°C and extension of the salinity gradient to the bottom layer in the water column, might be abnormal when compared to the conditions usually reported around Syowa Station (Wakatsuchi, 1982; Iwanami *et al.*, 1986; Satoh *et al.*, 1986; Fukuchi *et al.*, 1984, 1985). Nevertheless, the highest abundance of phytoplankton in the water column usually has been reported from the end of January to the beginning of February (Hoshiai, 1969; Fukuchi *et al.*, 1984; Iwanami *et al.*, 1986; Satoh *et al.*, 1986), as observed in this study. Satoh and Watanabe (1988) reported an increase of the relative importance of the phytoplankton as the primary producers in the summer season. Although the relationship between both communities, ice and sea water, in the ice covered area at the north of Syowa Station has been examined before (Hoshiai and Kato, 1961), it is still equivocal. Further investigations on composition and succession of phytoplankton species in both water and ice in relation to variables in the environmental conditions during the austral summer are needed to clarify the fate of the ice algae and the origin of the phytoplankton in the water column, leading to better understanding of the carbon cycle of the coastal ecosystem associated with ice in the Antarctic during the austral summer.

Acknowledgments

We are grateful to Profs. K. Moriwaki and K. Shibuya, the leaders of the 39th

Japanese Antarctic Research Expedition, for giving us helpful advice on the field work. We also express our thanks to the members of the 39th and 38th parties, especially Mr. A. Masuyama and Dr. K. Seto, respectively, for their cooperation in the field work. Thanks are due to the Hydrographic Department, Maritime Safety Agency, for lending us the CTD through the participation of Mrs. M. Yoritaka (39th party). We appreciate the kindness of Dr. K. Watanabe for providing us with information about the field work and for his guide to references. Our special thanks are extended to Dr. Harvey J. Marchant, Australian Antarctic Division, for his encouragement and critical reading of this manuscript.

References

- Burkholder, P.R. and Mandelli, E.F. (1965): Productivity of microalgae in Antarctic sea ice. *Science*, **149**, 872–874.
- Fukuchi, M., Tanimura, A. and Ohtsuka, H. (1984): Seasonal change of chlorophyll *a* under fast ice in Lützow-Holm Bay, Antarctica. *Mem. Natl Inst. Polar Res., Spec. Issue*, **32**, 51–59.
- Fukuchi, M., Tanimura, A. and Ohtsuka, H. (1985): Marine biological and oceanographical investigations in Lützow-Holm Bay, Antarctica. *Antarctic Nutrient Cycles and Food Webs*, ed. by W.R. Siegfried *et al.* Berlin, Springer, 52–59.
- Garrison, D.L. (1991): Antarctic sea ice biota. *Am. Zool.*, **31**, 17–33.
- Garrison, D.L. and Buck, K.R. (1985): Sea-ice algal communities in the Weddell Sea: species composition in ice and plankton assemblages. *Marine Biology of Polar Regions and Effects of Stress on Marine Organisms*, ed. by J.S. Gray and M.E. Christiansen. New York, J. Wiley, 103–122.
- Garrison, D.L. and Buck, K.R. (1989): The biota of Antarctic pack ice in the Weddell Sea and Antarctic peninsula regions. *Polar Biol.*, **10**, 211–219.
- Garrison, D.L., Sullivan, C.W. and Ackley, S.F. (1986): Sea ice microbial communities in Antarctica. *BioScience*, **36**, 243–250.
- Garrison, D.L., Buck, K.R. and Fryxell, G.A. (1987): Algal assemblages in Antarctic pack ice and in ice-edge plankton. *J. Phycol.*, **23**, 564–572.
- Hasle, G.R. and Syvertsen, E.E. (1997): Marine diatoms. *Identifying Marine Phytoplankton*, ed. by C.R. Tomas. San Diego, Academic Press, 5–385.
- Horner, R.A. (1985a): History of ice algal investigations. *Sea Ice Biota*, ed. by R.A. Horner. Boca Raton, CRC Press, 1–19.
- Horner, R.A. (1985b): Ecology of sea ice microalgae. *Sea Ice Biota*, ed. by R.A. Horner. Boca Raton, CRC Press, 83–105.
- Hoshiai, T. (1969): Seasonal variation of chlorophyll-*a* and hydrological conditions under sea ice at Syowa Station, Antarctica. *Nankyoku Shiryô (Antarct. Rec.)*, **35**, 52–67 (in Japanese with English abstract).
- Hoshiai, T. (1981a): Proliferation of ice algae in the Syowa Station area, Antarctica. *Mem. Natl Inst. Polar Res., Ser. E (Biol. Med. Sci.)*, **34**, 1–12.
- Hoshiai, T. (1981b): Solar radiation and stability of the undersurface of sea ice governing ice algal proliferation. *Nankyoku Shiryô (Antarct. Rec.)*, **73**, 23–29.
- Hoshiai, T. and Kato, M. (1961): Ecological notes on the diatom community of the sea ice in Antarctica. *Bull. Mar. Biol. Stn. Asamushi*, **10**, 221–230.
- Hoshiai, T. and Watanabe, K. (1996): A brief history of sea ice biota studies at Syowa Station and its vicinity. *Mem. Natl Inst. Polar Res., Spec. Issue*, **51**, 25–31.
- Iwanami, K., Futatsumachi, S. and Taniguchi, A. (1986): Short-term variation of chemical property of water and microplankton community in the coastal area near Syowa Station, Antarctica, in midsummer of 1984, I. chemical property including chlorophyll *a*. *Mem. Natl Inst. Polar Res., Spec. Issue*, **40**, 1–14.
- Landry, M.R. and Hassett, R.P. (1982): Estimating the grazing impact of marine micro-zooplankton. *Mar.*

- Biol., **67**, 283–288.
- Marchant, H. J., Watanabe, K. and Kawachi, M. (1996): Marine snow in Antarctic coastal waters. Proc. NIPR Symp. Polar Biol., **9**, 75–83.
- Medlin, L.K. and Priddle, J. (1990): Polar Marine Diatoms. Cambridge, British Antarctic Survey, 214 p.
- Parsons, T.R., Maita, Y. and Lalli, C.M. (1984): A Manual of Chemical and Biological Methods for Seawater Analysis. Oxford, Pergamon Press, 173 p.
- Richardson, M.G. and Whitaker, T.M. (1979): An Antarctic fast-ice food chain: observations on the interaction of the amphipod *Pontogeneia antarctica* Chevreux with ice-associated micro-algae. Br. Antarct. Surv. Bull., **47**, 107–115.
- Riebesell, U., Schloss, I. and Smetacek, V. (1991): Aggregation of algae released from melting sea ice: implications for seeding and sedimentation. Polar Biol., **11**, 239–248.
- Sasaki, H. and Hoshiai, T. (1986): Sedimentation of microalgae under the Antarctic fast ice in summer. Mem. Natl Inst. Polar Res., Spec. Issue, **40**, 45–55.
- Satoh, H. and Watanabe, K. (1988): Primary productivity in the fast ice area near Syowa Station, Antarctica, during spring and summer 1983/84. J. Oceangr. Soc. Jpn., **44**, 287–292.
- Satoh, H., Watanabe, K., Kanda, H. and Takahashi, E. (1986): Seasonal changes of chlorophyll *a* standing stocks and oceanographic conditions under fast ice near Syowa Station, Antarctica, in 1983/84. Nankyoku Shiryô (Antarct. Rec.), **30**, 19–32.
- Satoh, H., Watanabe, K. and Hoshiai, T. (1991): Estimates of primary production by ice algae and phytoplankton in the coastal ice-covered area near Syowa Station, Antarctica. Nankyoku Shiryô (Antarct. Rec.), **35**, 30–38.
- Simonsen, R. (1974): The diatom plankton of the Indian Ocean Expedition of R.V. “Meteor” 1964–65. Meteor Forschungsergeb. (D. Biol.), **19**, 1–66.
- Smith, W.O. and Nelson, D.M. (1985): Phytoplankton bloom produced by a receding ice edge in the Ross Sea: spatial coherence with the density field. Science, **227**, 163–166.
- Suzuki, R. and Ishimaru, T. (1990): An improved method for the determination of phytoplankton chlorophyll using N, N-dimethylformamide. J. Oceangr. Soc. Jpn., **46**, 190–194.
- Wakatsuchi, M. (1982): Seasonal variations in water structure under fast ice near Syowa Station, Antarctica, in 1976. Nankyoku Shiryô (Antarct. Rec.), **74**, 85–108.
- Watanabe, K. (1982): Centric diatom communities found in the Antarctic sea ice. Nankyoku Shiryô (Antarct. Rec.), **74**, 119–126.
- Watanabe, K. (1988): Sub-ice microalgal strands in the Antarctic coastal fast ice area near Syowa Station. Jpn. J. Phycol., **36**, 221–229.
- Watanabe, K. and Satoh, H. (1987): Seasonal variations of ice algal standing crop near Syowa Station, east Antarctica, in 1983/84. Bull. Plankton Soc. Jpn., **34**, 143–164.
- Watanabe, K., Satoh, H. and Hoshiai, T. (1990): Seasonal variation in ice algal assemblages in the fast ice near Syowa Station in 1983/84. Antarctic Ecosystems, Ecological Change and Conservation, ed. by K.R. Kerry and G. Hempel. Heidelberg, Springer, 136–142.

(Received October 13, 1999; Revised manuscript accepted February 7, 2000)